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SHORT NOTE

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Stable isotopes prove shell growth bands in the Antarctic bivalve *Laternula elliptica* to be formed annually

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Abstract Growth marks in calcareous shells or skeleton parts of benthic invertebrates are often assumed to be formed annually and hence are used for ageing purposes. For some Antarctic species this assumption has been validated by tagging experiments or direct monitoring of growth throughout the year. Here we use the record of stable isotope ratios ($\delta^{18}O$ and $\delta^{13}C$) deposited in shell carbonate of *Laternula elliptica* from King George Island to demonstrate that shell growth bands are formed annually in this species.

Introduction

Individual age is a key parameter of population dynamics. Age is required to establish growth and mortality patterns from which productivity of the population can be derived. Among those benthic organisms with calcareous shells or skeleton parts (e.g. corals, bryozoans, molluscs or echinoderms), many species exhibit growth band patterns. These bands are produced by alternate deposition of skeleton material of different density or structure. The alternation is triggered either by changes in environmental factors, such as temperature, salinity, oxygen or food supply or by internal factors such as reproduction (see e.g. Merrill et al. 1965; Thompson et al. 1980; Ebert 1988). These events may be part of a regularly repeated annual cycle, but they may also occur irregularly and non-predictably. Hence the growth band pattern itself neither tells us if the bands observed are formed at regular intervals in time nor how many bands are formed per year. Therefore an assumed annual growth band formation has to be validated by an independent approach.

Hitherto in the Antarctic, growth band formation has been validated in three benthic species either by tagging-recapture experiments or by year-round monitoring of growth: the bryozoan *Cellarinella watersi* (Barnes 1995), the bivalve *Yoldia eightsi* (Nolan and Clarke 1993; Peck and Bullough 1993), and the echinoid *Sterechinus antarcticus* (Brey et al. 1995) were proved to deposit growth bands annually. The growth marks in the shell of the brachiopod *Liothyrella uva*, however, were found to be formed at a rate of about one band per 1.8 years (Peck and Brey 1996).

Laternula elliptica (King and Broderip), a large (maximum length > 100 mm) and deep-burrowing bivalve, is widespread on muddy sediments around the Antarctic continent (Powell 1965). At some sites at the Antarctic islands (e.g. King George Island, Signy Island) it is a dominant species in terms of abundance and biomass (Everson and White 1969; Hardy 1972; Urban and Mercuri in press). The bivalve shows a distinct pattern of growth bands visible on the shell surface and in sections of the chondrophore that have been used for ageing purposes by Ralph and Maxwell (1977) and Urban and Mercuri (in press).

The ratio of the oxygen isotopes ^{18}O and ^{16}O ($\delta^{18}O$) in mollusc shell carbonate depends on seawater isotope composition and temperature during shell deposition. Deep ocean seawater isotope composition is stable on a biological time scale, and hence calcitic shell $\delta^{18}O$ can be related to ambient temperature via the paleotemperature equations of Epstein et al. (1953) and McCrea (1950). The ratio of the carbon isotopes ^{13}C and ^{12}C in shell carbonate is less temperature affected (Emrich et al. 1970), but depends mainly on changes in $\delta^{13}C$ of seawater bicarbonate mediated by primary production (Krantz et al. 1987). These relations can be used to derive environmental and ecological information from living or fossil calcareous species (see Krantz et al. 1987; Wefer and Berger 1991).

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Following the previous attempts of Jones et al. (1983), Krantz et al. (1984), Donner and Nord (1986) and others, we used oxygen and carbon isotope profiles in the shell to test whether or not growth bands are formed annually in *Laternula elliptica*. Because $\delta^{18}O$ of water is inversely related to temperature and $\delta^{13}C$ of dissolved inorganic carbon in pore and bottom waters is reduced during, or shortly after, periods of high primary production, we expected to find lower values in those parts of the shell deposited during spring/summer and higher values in shell material formed in autumn/winter.

Materials and methods

Specimens of *Laternula elliptica* were sampled at Potter Cove, a small inlet adjacent to Maxwell Bay, King George Island, Antarctica (62°14′ S, 58°40′ W) by scuba diving in 25-m water depth. Temperature in 25-m water depth ranges between + 1°C in February and < − 1.2°C in November (Klöser et al. 1993), but is likely to decrease to − 1.8°C during July/August, as observed at Signy Island (Clarke et al. 1988). Despite the glacier input in the cove, salinity remains between 34.0 ppt and 34.2 ppt in 25-m water depth (Klöser et al. 1993). There are no primary production data available from Potter Cove, but data from Admiralty Bay indicate a sharp peak of production in January/February (Domanov and Lipski 1990).

We selected several large (approx. 100 mm length) specimens from the samples, removed the soft parts and cleaned the shells with warm 5% NaOCl. After subsequent washing with 90% ethanol and drying, the shell surface was slightly ground. The shell of *Laternula elliptica* consists of two layers of which the outer one is very thin and fragile. On all valves examined parts of the outer layer were lost, mainly in the dorsal region. We selected the most intact valve (103 mm length, 63 mm height) for further analysis. Growth bands were counted at the shell surface and on a cross-section of the chondrophore. For isotope analysis, 43 carbonate samples of ca. 50 µg each were drilled from the outer shell layer in an equally spaced dorsal-to-ventral series using a small dental drill (bit size 0.5 mm).

Stable oxygen and carbon isotopes of the carbonate samples were measured with a Finnigan MAT251 mass spectrometer coupled to an automatic carbonate preparation device. Standard deviations of measurements are < 0.04‰ and < 0.06‰ for carbon and oxygen, respectively. Data are related to the Pee Dee belemnite (PDB) standard through repeated analyses of National Bureau of Standard isotopic reference material (NBS) 19 (Hut 1987).

Results

The shell surface of *Laternula elliptica* shows a ripple structure where wider crests alternate with narrower troughs. Occasionally a secondary pattern of fine parallel lines makes this structure difficult to detect, especially in the younger part of the shell. On the shell surface of the 1 valve selected for analysis we were able to identify 16 crests separated by 15 troughs. The examination of the chondrophore cross-section revealed a total of 21 wide bands corresponding to shell surface crests, i.e. 5 of these bands could not be identified clearly on the shell surface.

From the 43 carbonate samples, 1 (no. 11) was omitted from further analysis due to an insufficient amount of carbonate collected and 1 (No. 43) was omitted because it was contaminated with carbonate from the inner shell layer. Visual inspection of the shell showed 17 samples to be situated on a crest and 16 to be situated in a trough, whereas 7 samples could not be classified clearly. Both $\delta^{18}O$ and $\delta^{13}C$ values of crest samples were significantly lower than those of trough samples ($\delta^{18}O$ mean: 2.758 vs. 3.143, $P < 0.001$; $\delta^{13}C$ mean: 0.705 vs 1.125, $P = 0.037$), indicating that crests are deposited during spring/summer and troughs during autumn/winter. Figure 1 shows the complete $\delta^{18}O$ and $\delta^{13}C$ profiles.

Discussion

Our sample series (Fig. 1) does not show the clear picture of $\delta^{18}O$ and $\delta^{13}C$ profiles derived from other bivalve species, where a distinct wave pattern of rising and falling isotope values was observed (*Placopecten magellanicus*, Krantz et al. 1984; *Spisula solidissima*, Arthur et al. 1983, Jones et al. 1983; mytilide mussels, Donner and Nord 1986, Margosian et al. 1987). Moreover, the average difference in $\delta^{18}O$ measured be-

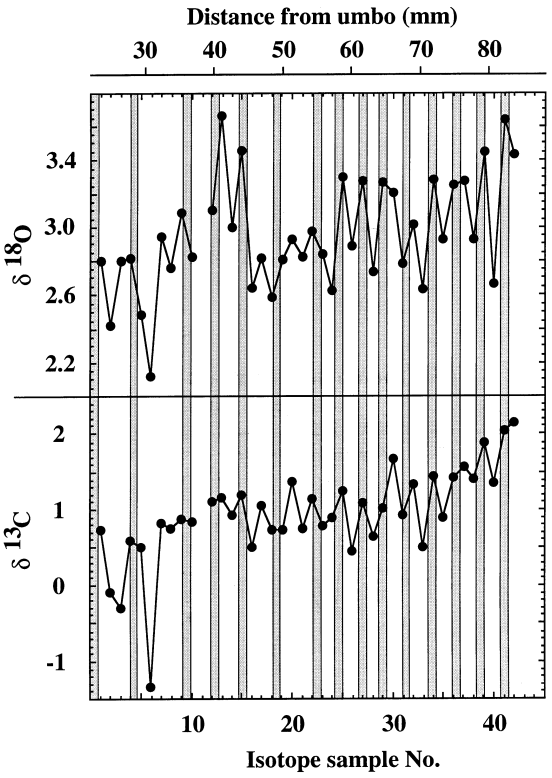

Fig. 1 $\delta^{18}O$ and $\delta^{13}C$ profiles along a dorsal-to-ventral transect in the outer shell layer of *L. elliptica*. Distance from umbo measured along the shell surface. Total distance from umbo to shell edge is 85.4 mm. Grey bars indicate positions of clearly identifiable winter growth bands (troughs)

tween crests and troughs is 60% lower than expected from a temperature difference of 2.8°C. This may be related to methodological shortcomings: compared to the species mentioned above, *Laternula elliptica* grows slowly and the distance between adjacent summer and winter growth bands is small. Obviously the resolution of our carbonate sample series is too coarse, and more, but smaller and closer spaced, samples would be required to achieve a clear separation of summer and winter growth bands and a better resolution comparable to the above examples. However, the statistical comparison of crest and trough data is still possible, and both the $\delta^{18}O$ and $\delta^{13}C$ data confirm that the shell growth bands of *Laternula elliptica* are annual markers: the crests are deposited during spring/summer and troughs are deposited during autumn/winter (Fig. 1). Hence, these growth bands can be used for age determination; however, the corresponding internal bands of the chondrophore provide a more reliable age estimate than the shell surface bands.

In contrast to the $\delta^{18}O$ record, there seems to be an overall trend of increasing $\delta^{13}C$ values with increasing size of the mollusc (Fig. 1), which may be caused by ontogenetic or environmental changes.

Ontogenetic trends in $\delta^{13}C$ have been observed in several mollusc species (see Krantz et al. 1987; Wefer and Berger 1991). They are assumed to be related to changes in metabolic activity such as maturation, which are known to affect the $\delta^{13}C$ record. However, in most examples presented in the literature, the general trend is towards lighter values during life. Only *Tridacna maxima* shows an ontogenetic shift towards heavier $\delta^{13}C$ similar to that seen in *Laternula elliptica*.

It is also possible that ventilation changes of bottom and pore waters occurred within the last 25 years, or a gradual change in phytoplankton species composition resulted in a different $\delta^{13}C_{\sum CO_2}$ composition of bottom waters. It might even be possible that a local change in bottom current velocity or direction caused a shift in the composition of organic detritus on the sea-floor. So a change from low $\delta^{13}C_{org}$ values to high values and – in turn – less depleted bottom water $\delta^{13}C_{\sum CO_2}$ values, and consequently higher $\delta^{13}C$ values in the bivalve shell may have occurred.

Seasonal changes in growth rate have been observed in many Antarctic species; however, it still remains unclear whether temperature or food supply is the main factor controlling growth (Clarke 1988; Brey and Clarke 1993; Nolan and Clarke 1993). Seasonal variability in food supply seems to be the more prominent environmental cycle (e.g. Clarke 1988; Matsuda et al. 1990; Wefer and Fischer 1991), because the annual temperature range (about 2.8°C in shallow waters around the Antarctic islands, less than 1°C at high-Antarctic sites) is very small compared to boreal areas. However, growth of calcareous shells may be decoupled from body growth, as observed in the brachiopod *Liothyrella uva,* which shows the highest shell growth rates during winter (Peck et al. in press) and no annual growth band formation (Peck and Brey 1996). Stable isotope ratios may help in the analysis of such difficult growth patterns in Antarctic benthic invertebrates.

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